INDIRECT AND DIRECT EFFECTS OF COMPETITOR PRESENCE ON BEHAVIOR OF INTRODUCED ANOLES IN HAWAIʻI

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Abstract

The intensity and frequency of aggressive behaviors are often used as evidence for interference competition. Much like the non-consumptive effects of predators on prey, competitor presence and/or costly aggressive interactions could have indirect effects on competitor behavior. Although phenomena consistent with competition between *Anolis carolinensis* and *Anolis sagrei* have been well documented, the mechanism driving the interaction is largely unknown and little work has examined the direct and indirect effects of competitor presence when these species co-occur. Using focal animal sampling, we compared time budgets of each species when housed in experimental mesocosms containing either one or both species. Interspecific aggression was not observed, suggesting that aggressive interference is not a mechanism driving competition. However, individuals of both species when in the presence of their competitor behaved differently compared to individuals in the absence of their competitor. Alterations in time spent engaged particularly in foraging and display behaviors could explain changes in population sizes and habitat use when these species co-occur and also suggests that multiple mechanisms, as opposed to just interference or exploitation, may be driving competition between *A. sagrei* and *A. carolinensis*.

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Introduction

Empirical patterns consistent with competition have been widely documented (Schoener 1983; Connell 1983; Gurevitch et al. 1992); however, studies that determined the mechanism of competition are rare (Tilman 1987; Stuart and Losos 2013). These mechanisms include indirect exploitative or direct interference interactions among competing organisms. Additionally, the behavioral, morphological, or physiological responses that drive competitive interactions are also infrequently determined (Tilman 1987). As the observable results of different species interactions may appear similar (e.g., exploitative competition and apparent competition), determining the mechanisms underlying species interactions can determine whether the patterns observed are due to competition or to non-competitive processes (Holt et al. 1994). By definitively determining the mechanism controlling a system, we can more accurately predict the outcome of species interactions (Tilman 1987; Holt et al. 1994).

A common approach to determining whether interference competition is occurring is to document interspecific agonistic interactions between competitors. Typically, a high frequency and/or intensity of interspecific aggressive behaviors are interpreted as evidence for interference competition (Primack and Howe 1975; Moore 1978; Tokarz and Beck 1987; Brown and Echternacht 1991; Hess and Losos 1991; Martin et al. 1996). For example, Primack and Howe (1975) examined how butterfly species altered their foraging behavior when hummingbirds were excluded. They documented that interference drove competition between butterfly and hummingbird species because hummingbirds aggressively chased butterflies away, preventing them from foraging on particular flowers. When interspecific agonistic behavior is not observed, this is interpreted as a lack of evidence for direct competition through interference interactions (e.g., Tokarz and Beck 1987; Wauters and Gurnell 1999).

However, avoidance of direct agonistic interactions with competitors could have individual- and population-level indirect effects, analogous to well-documented non-consumptive effects of predators (Lima and Dill 1990; Werner and Peacor 2003; Preisser et al. 2005). For example, elk alter their foraging behavior to minimize predation risk following wolf reintroduction, resulting in consumption of less nutritious diets and lower birth rates (Ripple et al. 2001; Hernández and Laundré 2005; Creel et al. 2007). The magnitude of the indirect effects of wolf presence on elk populations was similar in magnitude to the direct effect of wolf predation on elk (Creel and Christianson 2008). Similar indirect effects could occur because of competitor, as opposed to predator, presence. For example, organisms may decrease social or display behaviors out of fear that conspicuous signaling could alert competitors and result in costly interactions (Thornhill 1987; Kodric-Brown and Mazzolini 1992). Similarly, competing organisms may change movement or foraging behavior to avoid costly agonistic encounters over resources (Alatalo et al. 1985; Shealer and Burger 1993; Francini-Filho et al. 2010). By only looking for direct agonistic interactions, the indirect effects of competitor presence may be missed, thereby underestimating the role of interference competition. Time budgets remedy this issue and are particularly useful tools as they can quantify the entire behavioral repertoire (Newman 1956; Werner 1992; Walguarnery 2008).

Anolis lizards in the Greater Antilles are a textbook example of competition driving resource partitioning (e.g., Raven et al. 2011; Solomon et al. 2014; Bowman et al. 2017), yet the mechanism of competition is often unknown. Observational and experimental studies of anole competition have documented resource partitioning along three main axes—thermal habitat, structural habitat, and diet—to reduce competitive pressure (Rand 1967; Schoener 1968; Schoener 1970; Williams 1983; Pacala and Roughgarden 1985; Losos 1994; Kamath et al.

2013). For example, co-occurring anole species often consume different sizes and types of prey to reduce exploitation competition for food (e.g., Schoener 1968; Campbell 2000). Co-occurring anoles also often shift their habitat use (Schoener 1968; Losos et al. 1991). However, anoles cannot compete indirectly for thermal and structural habitat because they are mobile organisms that do not permanently occupy (i.e., deplete) space. Due to their territorial nature, however, anoles may interfere with one another for access to preferred thermal and structural habitats. Intraspecific interference is well-documented, with anoles fighting and displaying (i.e., head-bobs, push-ups, and dewlap extensions) to defend territories and resources from conspecifics (Evans 1938; Greenberg and Noble 1944; Stamps 1973; Stamps and Crews 1976). It is generally presumed that interspecific anole competition is largely via exploitation competition for prey, which in turn drives observed shifts in habitat use when anoles co-occur (Losos 2009). In actuality, there are few data addressing the relative importance of interspecific interference and exploitation in structuring anole communities (Losos 2009).

Of the studies documenting interference in anoles, the most data are available on interspecific agonistic interactions between two well-studied species, *Anolis carolinensis* and *Anolis sagrei* (Tokarz and Beck 1987; Brown and Echternacht 1991; Walguarnery 2008; Kamath et al. 2013). *Anolis carolinensis* is a trunk-crown microhabitat specialist (termed ecomorph), and has relatively shorter limbs, well-developed toe pads, and preference for trunk to canopy height perches, whereas *Anolis sagrei* is a trunk-ground ecomorph with relatively longer hind-limbs, poorly developed toe-pads, and a preference for broader and lower perches (Williams 1983; Mattingly and Jane 2004). Observational and experimental field studies have shown patterns consistent with competition whereby *A. carolinensis* moves to higher perches and declines in density when it co-occurs with *A. sagrei* (Collette 1961; Schoener 1975; Losos and Spiller 1999;

Campbell 2000; Walguarnery 2008; Edwards and Lailvaux 2012; Stuart et al. 2014). Although interspecific aggressive interactions are infrequently observed, the role of interference in natural settings is largely unknown because most studies have been conducted in lab settings on adult males (Tokarz and Beck 1987; Gerber and Echternacht 2000; Edwards and Lailvaux 2013; but see Walguarnery 2008). *Anolis* males are often the focus of studies since they defend territories more conspicuously and aggressively than females do (Stamps 1977b; Leuck 1995). As a result, inferences regarding the mechanisms driving species interactions are male-biased since female behavior is understudied. Similarly, although lab settings allow for increased control, lizards behave differently in lab than in natural settings (Brown and Echternacht 2001), so lab studies may not accurately reflect behavior in the field.

In this study, we compared time budgets of both males and females in experimental enclosures with different species assemblages to determine the role of interference in driving competition between *A. carolinensis* and *A. sagrei*. By comparing time budgets of each species in the presence versus absence of competitors, we aimed to 1) document the frequency and intensity of interspecific aggression and 2) determine the effect of competitor presence on behavior other than direct agonistic interactions. Given that competition between the two species is asymmetrical such that *A. carolinensis* is more negatively impacted compared to *A. sagrei* (Losos and Spiller 1999), if agonistic interactions are directly driving competition then we expect to see *A. sagrei* more frequently and aggressively initiate interspecific attacks. If avoidance of agonistic interactions is indirectly driving competition then we expect to see greater changes in time budgets of *A. carolinensis* when the two species co-occur.

Methods

Experimental Design

To document the effects of competitor presence on behavior, we used enclosures to create three lizard treatments: *A. carolinensis* alone, *A. sagrei* alone, and *A. carolinensis* with *A. sagrei*. Enclosures were 10 m x 10 m in area and built at the University of Hawaii Waimanalo Research Station on the island of Oahu, Hawaii, based on previous designs (Pacala et al. 1983). Each enclosure was established with the same number and type of plants commonly used as substrates by anoles in Hawaii to control for structural resource availability, and the lizards had access to ambient prey availability (Wright 2019). The experiment was replicated over time (n = 4), with each replicate using a new set of lizards collected from the same source populations from the University of Hawaii at Manoa campus. Each replicate ran for 61 days starting in June 2017, October 2017, February 2018, and June 2018. Individual lizards were permanently marked with VIE (visible implant elastomer; Northwest Marine Technology, Inc.), and marked with temporary dots of acrylic paint for identification. Lizards were randomly assigned to treatments with the contraint that lizards of the same sex and species assigned to the same treatment were within 10% snout-vent length of one another. Treatments were randomly assigned to enclosures with the constraint that an enclosure could not receive the same treatment on subsequent replicates. Initial lizard densities and sex ratios in each enclosure reflected natural variation (Schoener and Schoener 1980). Additional treatments with a third species (*Phelsuma laticauda*) are not reported here; however, these treatments required that the single-species treatments had nine individuals while the two-species treatments had eight individuals in order to keep total lizard density approximately constant across all treatments. Thus 104 lizards were used in the current study (26 per replicate).

Behavioral Observations

We used focal-animal sampling techniques via video recordings to observe lizard behavior. The observer would stand a minimum of 2 m from the focal lizard to limit observer-induced behaviors and used a Canon Vixia HF R700 video camera to film the lizard for a minimum of 5 minutes and a maximum of 20 minutes (Bloch and Irschick 2006; Edwards and Lailvaux 2012; Kamath et al. 2013). We used the program JWatcher (Blumstein and Evans 2006) to score the duration and frequency of behaviors in each video. The behaviors used to determine time budgets were adapted from an ethogram developed for *A. carolinensis* by Greenburg (1977). Behaviors were categorized into 1) states, or behaviors that have a duration and 2) events, or behaviors that are an occurrence (Altmann 1974). Table 1 shows the ethogram that was used.

Statistical Analysis

Time budgets were compiled separately for males and females of each species by averaging across individuals within each treatment by replicate combination. First, we combined all of the videos for each individual and summed the amount of time spent in each state behavior and the number of occurrences of each event behavior. We then divided these values by the total time that the individual was observed to calculate the proportion of time spent in state behaviors and the frequency of event behaviors. Each individual was a subsample; thus, we averaged these values across all individuals of the same species and sex that co-occurred within an enclosure during a replicate. This resulted in 32 time budgets (2 species x 2 sexes x 2 treatments x 4 replicates).

To detect shifts in time budget, we used permutational multivariate analyses of variance, PERMANOVA, with time budget as the response, and treatment (alone versus together), species, and sex as predictors. We included all three-way and two-way interactions among predictors in initial models. We used the function "adonis2" in R package vegan (R Core Team 2016; Oksanen et al. 2017), with permutations constrained by replicate. Time budget data were standardized by dividing each behavior by the maximum value for that behavior across all 32 time budgets (n = 4 replicates of species by sex by treatment combination). This standardization allowed us to combine state and event behaviors in one analysis. However, because time budgets typically look at state behaviors only, we conducted separate analyses for states and events combined, and for states only (hereafter combined time budget and states time budget, respectively). To test for homogeneity of multivariate dispersions, we used the function "betadisper" in R package vegan (R Core Team 2016; Anderson 2006). For data visualization, we conducted constrained analysis of principal coordinate analyses (CAP) using the function "capscale" in R package vegan and plotted the 32 time budgets in multivariate behavior space using ordination (R Core Team 2016; Oksanen et al. 2017).

We also conducted separate analyses on each behavior that we hypothesized could be impacted if lizards were avoiding interspecific agonistic interactions (i.e., indirect effects on behavior). The behaviors targeted were: *movement* as individuals may reduce movement to avoid potential encounters with competitors, *survey posture* which is used by anoles for both sit-and-wait foraging and for vigilance against predators and intruders (Stamps 1977a), *looking* as another form of vigilance, *eating* since anoles may compete for food, and *displaying* and *dewlapping* which are both used in visual communication.

The state behaviors *movement* and *looking* occurred in over 98% of videos; therefore, we were able to fit linear mixed models with logit transformed proportion of time engaged in the behavior as the response (Warton and Hui 2011), with treatment (alone versus together), species, and sex and their interactions as fixed effects, as well as replicate as a fixed effect. We included as random effects date (as an integer) to account for similar conditions for videos recorded on the same day, enclosure to account for similarities among videos recorded in the same enclosure, and lizard ID to account for repeated measurements of individuals. To account for variation in total time of each video observation, we weighted each observation using the scaled video time. Models were fit using the function "lmer" in the R package lme4 (Bates et al. 2015; R Core Team 2016), and hypothesis tests were conducted via the Satterthwaite approximation for degrees of freedom using the "anova" function in the R package lmerTest (Kuznetsova et al. 2016; R Core Team 2016).

The remaining behaviors occurred more rarely (18-60% of videos), and as a result we could not generate satisfactory model convergence using the same approach as for *movement* and *looking*. Instead, we used a two-step hurdle model approach (Mullahy 1986) whereby we first asked whether there was a treatment effect on the probability of the behavior occurring (i.e., using all video observations), and then asked whether there was a treatment effect on the duration of the state behavior or frequency of the event behavior given that it was observed (i.e., using only videos in which the behavior of interest was observed). This procedure was as follows.

First, for each behavior we scored whether it occurred in each video, creating a binomial data set. We then fit generalized linear mixed models separately for each behavior with occurrence of the behavior as the response (0, 1), and treatment (alone versus together), species,

and sex and all interactions as fixed effects. We also included replicate as a fixed effect, and we included as random effects enclosure to account for similarities among videos recorded in the same enclosure and lizard ID to account for repeated measurements of individuals. Date (as an integer) was also included as a random effect to account for similar conditions for videos recorded on the same day in all models except the *displaying* model due to convergence issues. We used a binomial distribution with a complementary log-log link and the total time included in each video observation as an offset to account for the binomial nature of the data set and the fact that each video varied in duration (Bolker 2014). These models were fit using the function "glmer" in the R package lme4 (Bates et al. 2015; R Core Team 2016). Hypothesis tests were conducted using likelihood ratio tests. We then fit separate models using only videos in which the behavior occurred to determine whether there were treatment effects on behavior duration (*survey posture*: 332 videos, 76 lizards; *displaying*: 291 videos, 63 lizards, *eating*: 89 videos, 49 lizards; *dewlapping*: 223 videos, 53 lizards). For state behaviors (*survey posture*, *displaying*, *eating*), these models had the same structure as the models used for *movement* and *looking* (see above). For the event behavior *dewlapping*, we fit a generalized linear mixed model with the number of dewlaps observed during a video as the response, and treatment (alone versus together), species, and sex and all interactions as fixed effects. Replicate was also a fixed effect. In addition to including enclosure and lizard ID as random effects as outlined above (we were unable to include date because of convergence issues), we also included an observation-level random effect to account for overdispersion, a Poisson distribution because the response is a count, and video duration as an offset because each video observation varied in length of time lizards were in sight (Crawley 2007; Harrison 2014; Bates et al. 2015). This model was fit as above. For all analyses, we examined the distribution of residuals and plotted the fitted values

against the residuals to check model assumptions. Analyses proceeded as described since model assumptions were not met when fitting negative binomial or gamma models.

Results

In total, we collected 140.9 hours of video, which yielded 120.9 hours in which lizards were in sight and behaviors were recorded. Mean video length was 17.3 ± 4.8 minutes, with 5.96 ± 6.31 videos recorded per individual and 11.7 ± 8.2 hours of video per enclosure per replicate. Raw data time budgets for each sex and species in the two treatments can be found in the Appendix (Appendix Figures A2-A3).

Direct Agonistic Interactions

Aggressive interactions (i.e., attacks) were rare, with only one instance of interspecific aggression observed out of 43.8 hours of video from the together treatment. In this attack, a male *A. sagrei* finished copulating then displayed at, lunged toward, and bit a displaying male *A. carolinensis* that had been within 50 cm, and the interaction lasted 4 seconds. All other attacks were intraspecific: a male *A. carolinensis* attacking another male *A. carolinensis* in the together treatment (n = 1), a male *A. sagrei* attacking another male *A. sagrei* in the alone treatment (n = 2), and a female *A. sagrei* attacking a male *A. sagrei* during copulation in the alone treatment (n = 3). *Anolis sagrei* initiated most of the attacks (6/7, 86%).

Combined Time Budget

We did not observe shifts in the combined time budget due to treatment effects (*treatment* $F_{1,25} = 1.4$, $p = 0.18$) and preliminary analyses found no statistically significant interactions.

However, there were differences in the time budgets of the two species and between the two sexes evident from significant PERMANOVA analyses (*sex* $F_{1,25} = 2.9$, $p = 0.003$, Figure 1a; *species* $F_{1,25} = 5.8$, $p = 0.001$, Figure 1b) and non-significant betadispers (*sex* $F_{1,30} = 0.598$, $p = 0.445$; *species* $F_{1,30} = 0.343$, $p = 0.563$). We interpreted how these groups differed in multivariate behavior space by visualizing the results of the CAP using ordination plots (Figure 1). The first two axes each explained 12% of the variation. *Anolis carolinensis* spent more time moving and more frequently eyespotted and changed color, whereas *A. sagrei* dewlapped and displayed more often or longer than *A. carolinensis*. Females looked longer than males, and males tended to squirrel and dewlap more frequently and display longer than females.

States Time Budget

The analysis of the states budget explained more variation than the analysis of the combined time budget: the first two CAP axes explained 21% and 19% of the variation, respectively. There was a non-significant trend towards competitor presence causing the species to shift their time budgets in different ways (*treatment*species* PERMANOVA $F_{1,22} = 1.9$, $p = 0.083$, Figure 2a; betadisper $F_{3,28} = 0.289$, $p = 0.833$). Both *A. sagrei* and *A. carolinensis* in the absence of their competitor cover larger portions of multivariate behavior space compared to the same species in the presence of their competitor. For *A. sagrei,* time budgets in the together treatment showed less dispersion and occurred within the region used in the alone treatment. In contrast, dispersion was similar across treatments for *A. carolinensis* but there was a shift in multivariate behavior space as they spent more time looking and mating in the together treatment and more time eating and moving in the alone treatment. The sexes responded differently to competitor presence (*treatment*sex* PERMANOVA $F_{1,22} = 2.3$, $p = 0.045$, Figure 2b; betadisper

$F_{3,28} = 0.0698$, $p = 0.976$). Males in the together treatment engaged in a subset of the behaviors of males in the alone treatment (less dispersion), while females shifted their time budgets (Figure 2b). Males in the alone treatment spent more time displaying and in survey posture, and used a larger portion of multivariate behavior space than males in the together treatment. Females in the alone treatment spent more time eating and moving than females in the together treatment, resulting in a shift in position in multivariate behavior space. There was an interaction between species and sex (*species*sex* PERMANOVA $F_{1,22} = 2.7$, $p = 0.015$, Figure 2c; betadisper $F_{3,28} = 0.794$, $p = 0.507$) such that *A. carolinensis* males engaged in a subset of behaviors that *A. carolinensis* females performed, while *A. sagrei* males differed from females in multivariate behavior space by spending more time displaying and in survey posture.

Single Behavior Analyses

Anolis sagrei were less likely to be observed eating in the together treatment (*treatment*species* $\chi^2 = 8.4$, df = 1, $p < 0.01$; Figure 3a). When eating was observed, females spent more time eating than males (*sex* $F_{1,80.7} = 6.3$, $p = 0.014$; Figure 4c). There was an interaction between treatment and sex such males were less likely to be observed in survey posture in the together treatment (*treatment*sex* $\chi^2 = 5.1$, df = 1, $p = 0.02$; Figure 3b). A range of differences in the percent of time spent in survey posture was seen between the together and alone treatments (*treatment*species*sex* $F_{1,43.4} = 4.1$, $p = 0.049$): female *A. sagrei* decreased, female *A. carolinensis* and male *A. sagrei* increased, and male *A. carolinensis* did not change (Figure 4d). For dewlapping, there was a non-significant treatment by sex interaction such that the together treatment males were less likely to dewlap and females were more likely to dewlap (*treatment*sex* $\chi^2 = 3.6$, df = 1, $p = 0.058$; Figure 3d). When dewlapping was observed, there

was a trend towards males decreasing dewlap frequency when in the together treatment whereas female dewlap frequency trended towards increasing (*treatment*sex* $\chi^2 = 3.7$, df = 1, p = 0.054).

Additional patterns were observed regarding sex and species differences. *Anolis sagrei* were more likely to be observed displaying and dewlapping compared to *A. carolinensis*, and males were more likely to be observed displaying and dewlapping than females (*displaying*: *species* $\chi^2 = 38.4$, df = 1, $p < 0.01$; *sex* $\chi^2 = 6.2$ df = 1, p = 0.01; *dewlapping*: *species* $\chi^2 = 39.7$, df = 1, $p < 0.01$; *sex* $\chi^2 = 33.6$, df = 1, $p < 0.01$; Figures 3c and 3d). When display behavior and dewlapping were observed, males displayed and dewlapped more than females and *A. sagrei* displayed and dewlapped more than *A. carolinensis* (*displaying*: *species* $F_{1,44.2} = 8.8$, $p < 0.01$; *sex* $F_{1,33.6} = 27.8$, $p < 0.01$; *dewlapping*: *species* $\chi^2 = 13.4$, df = 1, $p < 0.01$; *sex* $\chi^2 = 35$, df = 1, $p < 0.01$; Figure 4e and 4f). *Anolis carolinensis* spent more time moving and looking than *A. sagrei* (*moving*: *species* $F_{1,25.1} = 70.8$, $p < 0.01$; *looking: species* $F_{1, 48.1} = 12.6$, $p < 0.01$; Figure 4a and 4b) and females spent more time looking (*sex* $F_{1,39} = 4.7$, p = 0.04; Figure 4b) than males.

Discussion

While interspecific aggression was rare, the states time budget and single behavior analyses suggest that there are indirect effects of competitor presence through behavioral shifts when *A. carolinensis* and *A. sagrei* co-occur. The rarity of direct aggression in our observations supports previous work showing the limited role of interference competition between these two species. During staged lab encounters, Walguarnery (2008) and Edwards and Lailvaux (2013) observed similarly low attack frequencies and Tokarz and Beck (1987) recorded reduced aggressive behaviors in both species when in the presence of their competitor. In field settings, Brown and Echternacht (1991) also rarely observed aggressive behavior during naturally-

occurring and staged field encounters between male *A. sagrei* and male *A. carolinensis*. Our results provide field-based, non-staged support to the hypothesis that direct interference does not drive competition between *A. carolinensis* and *A. sagrei.*

Our results captured behavioral shifts in time budget resulting from competitor presence, as well as non-significant but suggestive trends in other behaviors, that are consistent with the phenomena of competition observed in this system. Recall that *A. carolinensis* population densities decrease and they shift their habitat use to occupy higher perches when in the presence of *A. sagrei*; *A. sagrei*, however, is less affected by the co-occurrence. From the states time budget analyses, we observed *A. carolinensis* shifting behaviors they engage in whereas *A. sagrei* performed a subset of its behaviors when in the presence of the competitor. This pattern is consistent with asymmetrical competitive interactions documented in other species in which the less successful species shifts its behavior in concordance with shifts in its habitat or resource use to reduce competitive stress and interactions with its competitor (e.g., Namgail et al. 2007; Harrington et al. 2009). Consistent with this expectation, we documented larger alterations in the behavior of *A. carolinensis* because *A. sagrei* is the dominant competitor. The results from the single behavior analyses can add further insight to the nature of the time budget shifts by splitting the behaviors into two suites: those involved with social behaviors (displaying and dewlapping) and those involved with foraging and vigilance (survey posture, eating, moving, and looking).

Competitor presence affected social behavior in ways that suggest *A. carolinensis* and *A. sagrei* may be using social behaviors for heterospecific communication to establish and defend territories and could explain the resource use shifts and population density alterations observed when these species co-occur. Introduction of a competitor can be predicted to alter social

behavior in three ways: 1) the focal anole may decrease the time spent in social behavior for fear of attracting unwanted, costly attention from the competitor; 2) it may not alter the time spent engaged in social behavior as it does not recognize the introduced lizard as a threat; and 3) it may recognize the introduced competitor as a threat and increase its engagement in social activities to protect its territory from the unknown, novel intruder. Given the substitutive design of our experiment, in which total lizard density was controlled across enclosures and therefore the intraspecific density in the together treatment was roughly half of the intraspecific density in the alone treatment, we would expect the following patterns under each scenario. If anoles do not act territorially towards heterospecifics and display only towards conspecifics (Jenssen 1977), we would expect to see them engaged in social behaviors less in the together treatment than in the alone treatment because conspecific density was reduced by half. If anoles use social behaviors for heterospecific and conspecific communication however, we would expect the amount of time engaged in social behaviors to be equal between treatments if heterospecifics are perceived as an equal threat, or even greater in the together treatment if heterospecifics are perceived as a greater threat. Contrary to Jenssen (1977), our findings support this latter scenario as social behavior frequency and duration generally did not differ between treatment types, meaning that the anoles engaged in social behaviors more than expected if social displays were strictly for conspecific communication. This finding is particularly striking when also considering that both aggression and social display behaviors are used for territoriality and resource defense in these lizards. Because the cost of aggressive encounters (especially if injuries are incurred) is higher than the cost of engagement in other social behaviors, we would assume that animals would use the most cost-effective strategy to defend territories and reduce competitive stress (Clutton-Brock et al. 1979; Hack 1997). We would also expect that the species that more frequently engages in social

behaviors would better sustain and occupy a preferred territory and encourage competitors to either leave the area or risk engagement in costly aggressive interactions. The rarity of aggression conforms to this expectation. We also observed *A. sagrei*, the more dominant competitor, engaging in display behavior for longer and dewlapping more than *A. carolinensis* (Figures 4e and 4f). This trend is consistent with expectation since in previous studies the dominant competitor, *A. sagrei*, engaged in social displays more than the more highly impacted species, *A. carolinensis*, and the more highly impacted species also shifted its habitat use to avoid competitive pressures (Collette 1961; Schoener 1975; Campbell 2000; Walguarnery 2008; Edwards and Lailvaux 2012; Stuart et al. 2014). Therefore, not only does competitor presence indirectly affect engagement in social behaviors, but *A. carolinensis* and *A. sagrei* are competing species that potentially use heterospecific communication to reduce competitive stress. Future work examining the effect of additive designs and conspecific versus heterospecific densities on social behaviors should be conducted to confirm the trends of indirect effect of competitor presence on social behavior suggested by this study.

Indirect effects of competitor presence on foraging and vigilance behavior also support patterns consistent with competition. *Anolis sagrei* is a sit-and-wait predator (Johnson et al. 2008) while *A. carolinensis* is an active forager (Nunez et al. 1997). If these species compete for food, as many studies suggest (Collette 1961; Schoener 1975; Losos 1994; Campbell 2000; Stuart et al. 2014), we may expect to see alterations in time spent eating, looking, and/or in survey posture, as these behaviors are associated with foraging in anoles. Although our single behavior analyses only showed treatment effects on survey posture, the non-significant trends affiliated with eating and looking as well as the significance of the interaction between treatment and species in the states time budget confirm this expectation. We probably only detected

treatment significantly affecting survey posture since more data was collected for this behavior than for the other behaviors. Typical of anoles, both species spent a majority of their time (approximately 40-75%) engaged in survey posture (Figure 5d and Appendix Figure A2; see Stamps 1977a), whereas the lizards rarely engaged in the other behaviors (e.g., spending less than 10% of their time eating when eating was observed). Although exhibiting different foraging tactics, both species showed a trend towards reducing the amount of time spent eating when in the presence of their competitor (Appendix Figure A1), suggesting that competitor presence may be altering foraging behavior. Although a statistically non-significant trend, it is consistent with the negative impacts of competition, particularly in *A. carolinensis*, when these species co-occur as well as past work examining the role of food competition and exploitation as the mechanism driving competition between these species. *Anolis carolinensis* and *A. sagrei* have overlapping diets, consuming similarly sized prey from the same taxa (Schoener 1968; Campbell 2000), and competitor presence is speculated to drive down prey populations. We would expect to see a reduction in the time spent eating, as observed in this study, due to a reduction in prey availability. Therefore, the behavioral shifts we observed are consistent with two likely non-mutually exclusive concepts: 1) competitor presence indirectly affects behavior since anoles altered their behavior to avoid costly aggressive interactions, and 2) anoles are likely engaging in exploitative competition over prey, which is again reflected in alterations in behavior when the competitor is present. Additional studies experimentally altering prey densities or documenting diet shifts as well as fecundity, parentage, and offspring production of both species in the presence versus in the absence of their competitor should be conducted to determine the magnitude of the effect of competitor presence.

Overall differences in how the sexes behaved corroborates the known natural histories of these species. The sexes differed in both their combined time budgets (Figure 1a) and engagement in individual behaviors. For example, males engaged in social display behaviors more frequently or for longer than females. This finding is consistent with past studies (Nunez et al. 1997; Jenssen et al. 2000) and is likely due to male use of social displays to defend territories and attract potential mates whereas female use of social displays is to predominantly defend resources. We also observed females eating for longer periods than males, which is consistent with past work in many anole species (Andrews 1971; Fleming and Hooker 1975; Lister and Aguayo 1992; Preest 1994). One explanation for this observed difference is that the sexes differ in their energy requirements as female reproduction is more energetically costly than male. Eating time may have also differed due to the size of the prey items consumed. Anoles are gape-limited predators and females typically consume smaller prey due to their smaller head size compared to males (Schoener 1968; Fleming and Hooker 1975). It is therefore possible, though unlikely, that the prey items available in the enclosures were appropriately sized for males but slightly too large for females, hence the increased eating time. Further examination of the gut contents and prey items consumed by anoles recovered at the end of each experimental replicate as well as quantification of the prey availability in the enclosures should be conducted. Differences between the sexes and the frequency by which we observed females shifting their behavior due to competitor presence compared to males also supports the hypothesis Edwards and Lailvaux (2013) proposed that female behavior may be more important than male behavior in driving competition between *A. carolinensis* and *A. sagrei*. Future work incorporating female anoles needs to be conducted to avoid male-biased results and further test this hypothesis. Most notably though, our time budget is consistent with past natural history work conducted on *A.*

carolinensis, one of only six anole species to have had their time budget documented (see Andrews 1971; Fleming and Hooker 1975; Talbot 1979; Lister and Aguayo 1992; Jenssen et al. 1995; Nunez et al. 1997). This suggests that our work accurately captures how these lizards behave and, in addition to corroborating known biological and behavioral trends, provides the first accurate time budget for *A. sagrei*.

To conclude, the findings of this study suggest that although *A. carolinensis* and *A. sagrei* do not aggressively interfere with one another, competitor presence does indirectly affect behavior. Direct aggressive behavior was rarely observed, yet the indirect effects of competitor presence cannot be ruled out as a possible mechanism contributing to competition between *A. carolinensis* and *A. sagrei*. Although often statistically non-significant, behaviors related to foraging, vigilance, and social interactions in both species changed because of competitor presence. In addition to being consistent with the past work documenting exploitative competition and the hypothesis that anoles predominantly partition resources to reduce competition over prey (Collette 1961; Schoener 1975; Losos 1994; Campbell 2000; Stuart et al. 2014), the effects of competitor presence on behaviors related to foraging (i.e., survey posture and eating) also suggest that multiple mechanisms may actually drive competition in this system (i.e., exploitation and indirect effects). Moreover, the differences between the sexes and the greater frequency of females altering their behavior when in the presence of their competitor compared to males suggests that more effort should focus on documenting the role of females in the competitive interactions between *A. carolinensis* and *A. sagrei* (Edwards and Lailvaux 2013). Ultimately, our experimental determination of the prevalence of interference and the indirect effects of interference on anole behavior demonstrate that competitor presence does indirectly alter behavior and that interference due to competitor presence cannot be excluded as a driver of

competition in this system. Determination of the potential indirect effects of competitors on behaviors needs to be more regularly examined across taxa since such findings can corroborate or provide further explanations for the outcomes of species interactions.

Tables

Table 1. Ethogram of state and event behaviors of *Anolis carolinensis* and *Anolis sagrei*.

STATE BEHAVIORS

1. **Move**: a run, walk, crawl, stalk, or drag motion
2. **Display**: display behavior that includes both head bobs (repeated movement of head up and down such that only head and neck move and the tail does not lift up) and push-ups (repeated raising and lowering of individuals' body through the use of pushing with the forelimbs; tail will also flex up and down and body is relatively rigid)
3. **Mating**: copulation between female and male lizard
4. **Eating**: handling time required to fully consume prey items or shed skin
5. **Look**: turning or slight cocking of the head to survey surroundings
6. **Survey posture**: vertical positioning of a lizard such that the head is pointing towards and is nearer the ground than the tail
7. **Curl**: positioning the body in a C-like shape

EVENT BEHAVIORS

1. **Squirrel**: quick lateral movement on a substrate, typically while perched vertically on the substrate
2. **Jump**: movement of body into air to get from one substrate to another
3. **Attack**: aggressive interaction between two individuals, usually involving biting and physical attack
4. **Dewlap**: extension of gular flap
5. **Gape**: opening of mouth wide, tongue typically does not extend past edge of mouth
6. **Air lick**: extending of tongue outside of mouth
7. **Tongue touch**: extension of tongue such that it touches a substrate
8. **Tail wag**: side-to-side motion of tail
9. **Color change**: change in skin color, either increase or decrease in skin pigmentation
10. **Eyespot**: darkening of skin pigment immediately posterior of the eye
11. **Stretch**: extension of a limb away from the body so that the appendage is not bent
12. **Leg raise**: lifting of any one leg, hind or front, into the air
13. **Egg laying**: depositing of egg for external incubation

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Figures

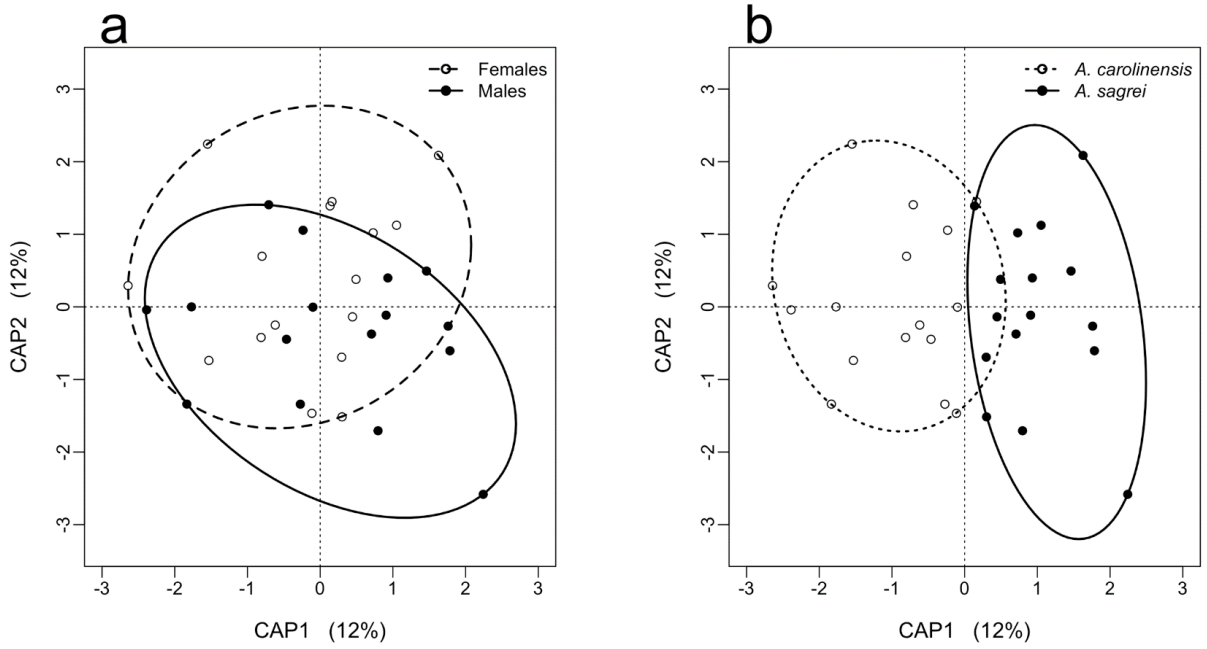

Figure 1. Constrained analysis of principle coordinates analysis ordination plot of combined time budget (i.e., state and event behaviors) by a) sex and b) species. Displaying and dewlapping positively load on whereas moving, eyespotting, and color changing negatively load on CAP1. Looking positively loads on CAP2 while squirreling, dewlapping and displaying negatively load on CAP2.

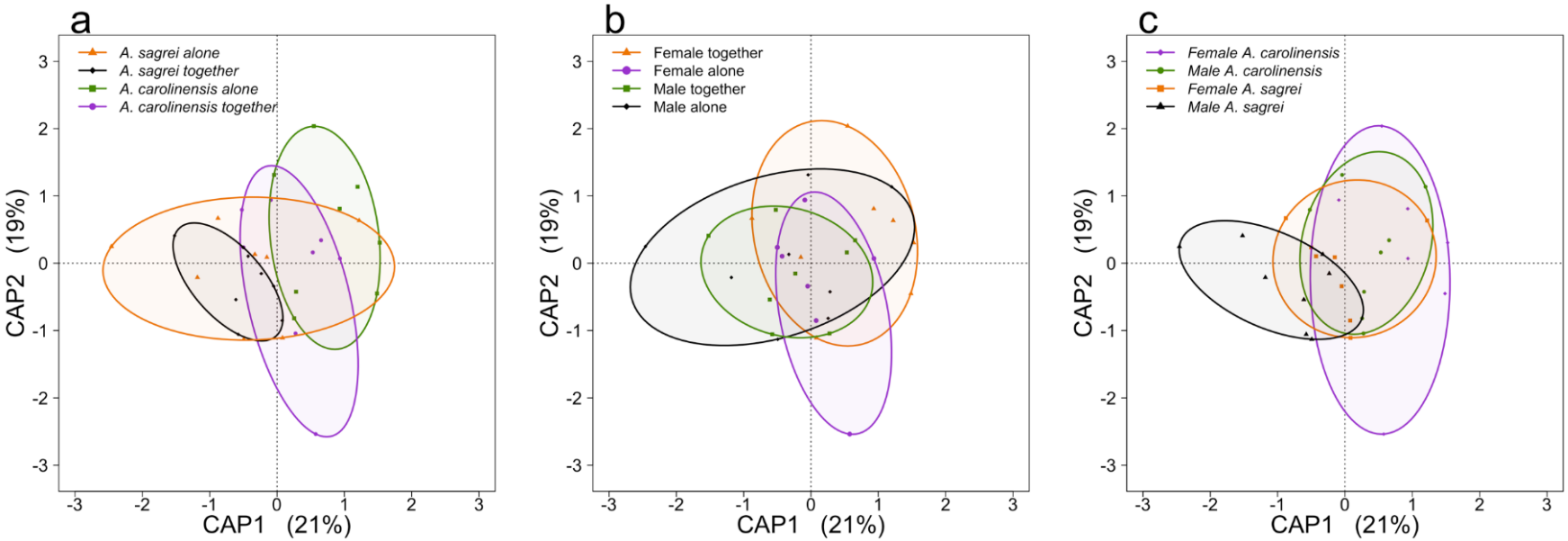

Figure 2. Constrained analysis of principle coordinates analysis ordination plot of state behaviors only time budget by a) treatment*species, b) treatment*sex, and c) species*sex. Looking, eating, and moving positively load on CAP1 and displaying negatively loads on CAP1. Eating and moving positively load on CAP2 while looking and mating negatively load on CAP2.

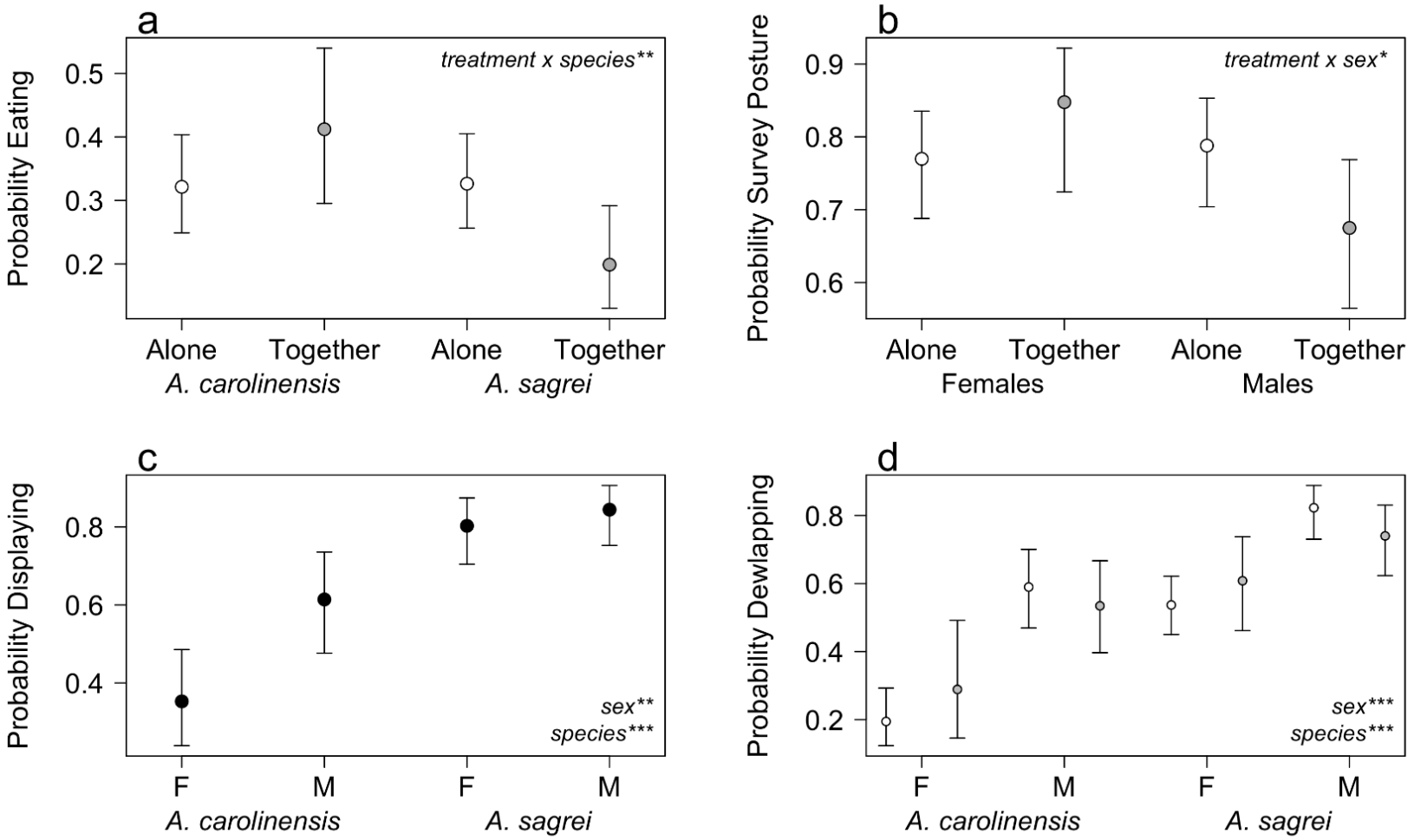

Figure 3. Probability of observing the following behaviors in a particular video bout: a) eating, b) survey posture c) displaying, d) dewlapping. Open circles signify the alone treatment and filled gray circles signify the together treatment. Shown are fitted effects (± 95% confidence intervals) from the model described in the text. Asterisks indicate significance of plotted relationships (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$) and NS indicates $p > 0.05$.

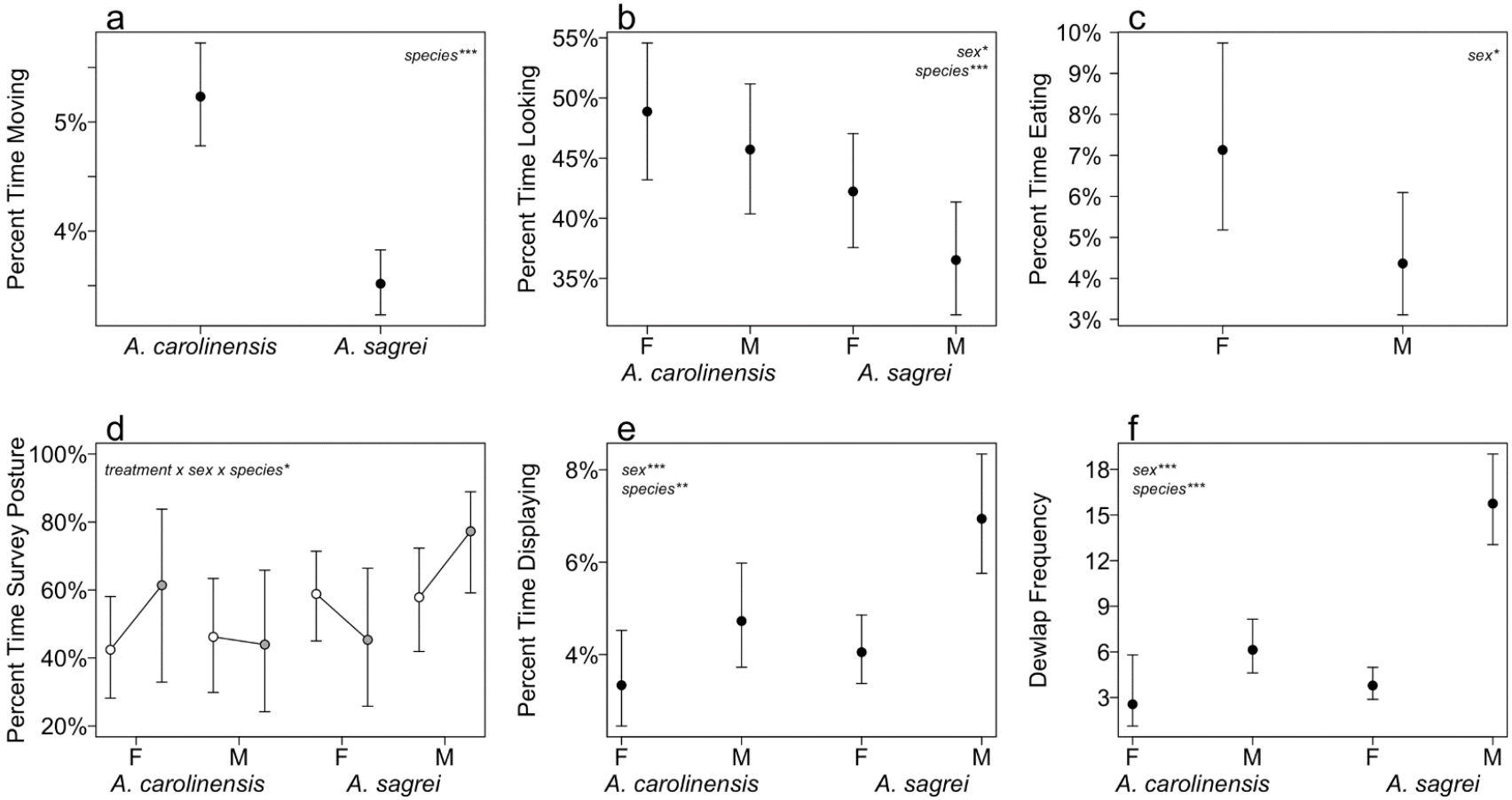

Figure 4. Percent of time anoles spent a) moving, b) looking, c) eating, d) in survey posture, e) displaying and the frequency of f) dewlaps for every 15 minutes of observation. Panels a-b include data from all videos whereas panels c-f include only videos where the behavior was observed. Open circles signify the alone treatment and filled gray circles signify the together treatment. Shown are fitted effects (± 95% confidence intervals) from the model described in the text. Asterisks indicate significance of plotted relationships (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$) and NS indicates $p > 0.05$.

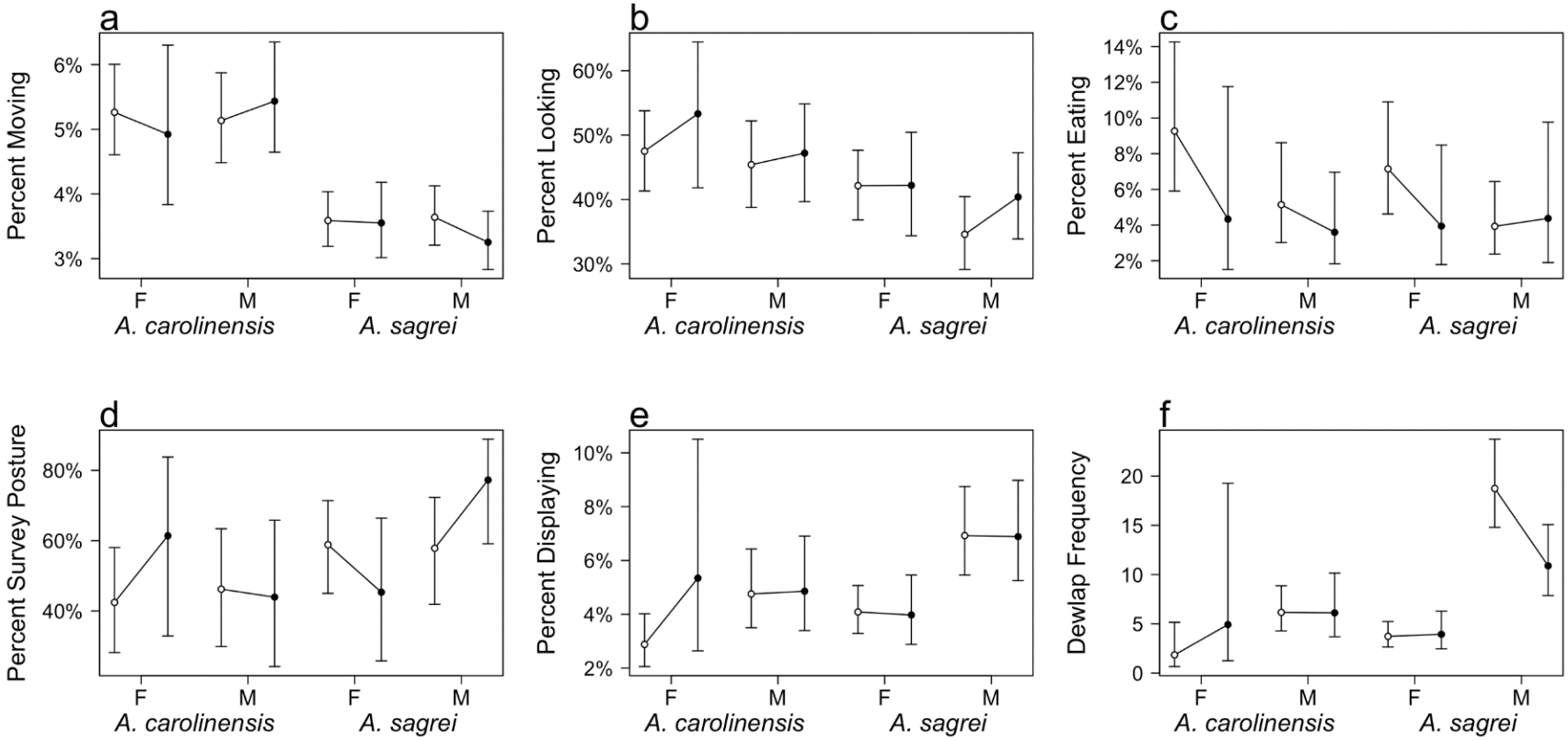

Figure 5. Percent of time anoles spent a) moving, b) looking, c) eating, d) in survey posture, e) displaying and the frequency of f) dewlaps. Panels a-b include data from all videos whereas panels c-f include only videos where the behavior was observed. Open circles signify the alone treatment and filled circles signify the together treatment. Shown are fitted effects (± 95% confidence intervals) from the model described in the text. Asterisks indicate significance of plotted relationships (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$) and NS indicates $p > 0.05$.

Appendix

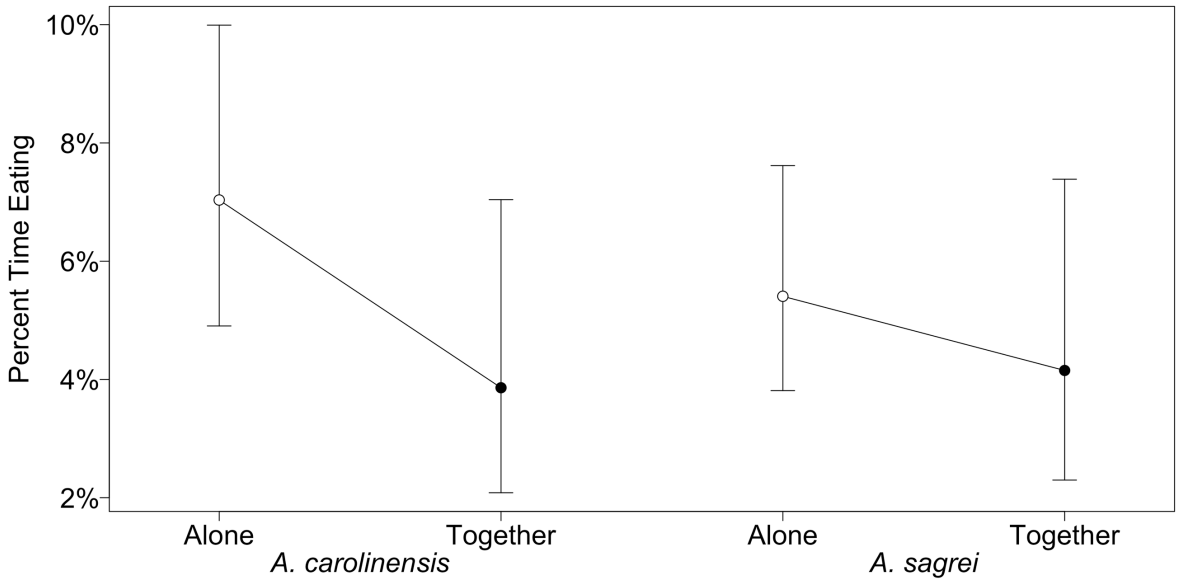

Figure A1. Percent of time anoles spent eating from videos where the behavior was observed. Shown are fitted effects (± 95% confidence intervals) from the model described in the text. Open circles signify the alone treatment and filled circles signify the together treatment.

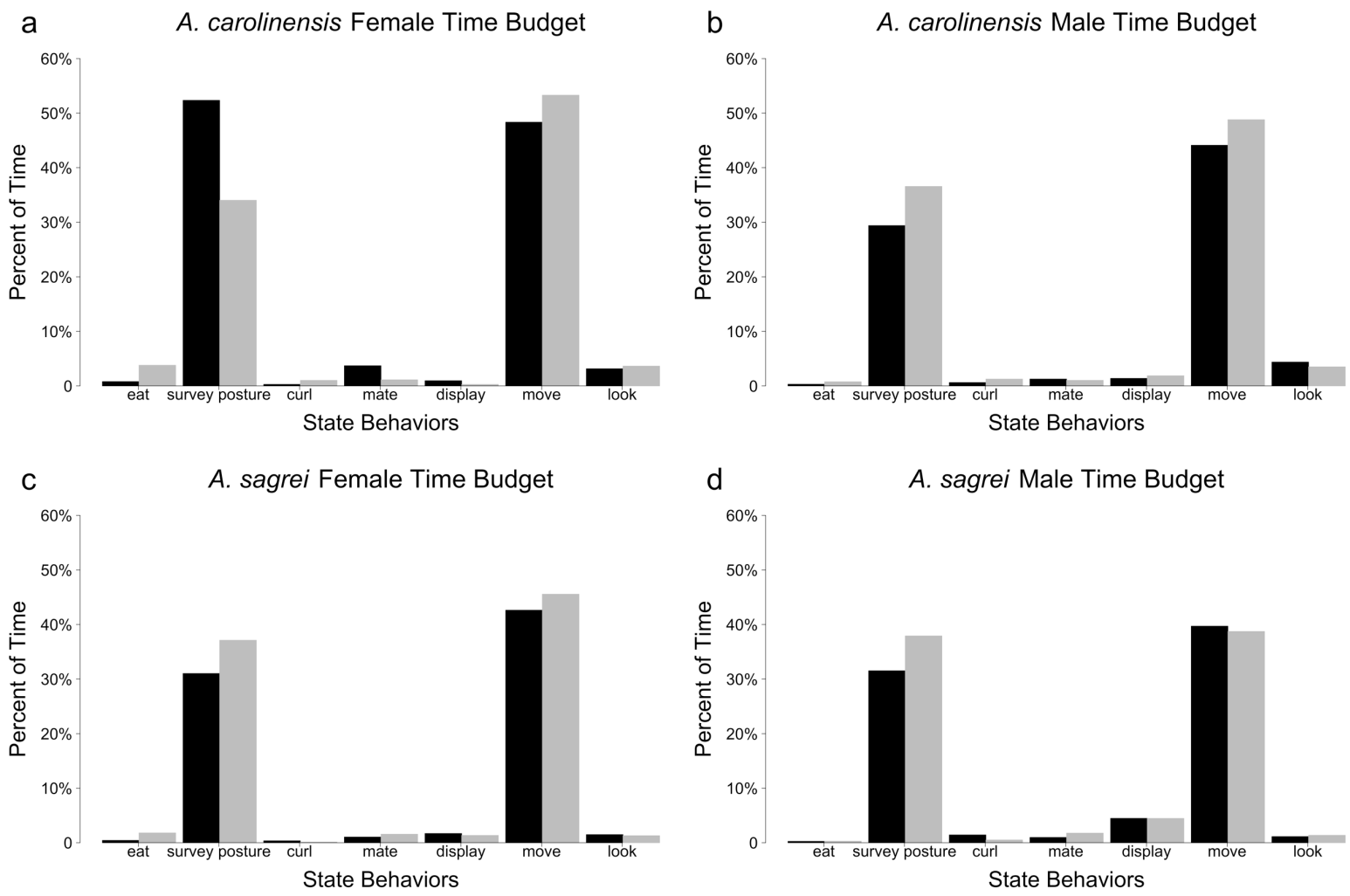

Figure A2. State behavior time budgets for male and female *A. carolinensis* and *A. sagrei*. The black bars represent the proportion of time engaged in a behavior in the presence of the competitor and the gray bars represent the proportion of time in the absence of the competitor. Bars will add up to greater than 100% as lizards could engage in multiple behaviors at once, i.e., displaying while in survey posture.

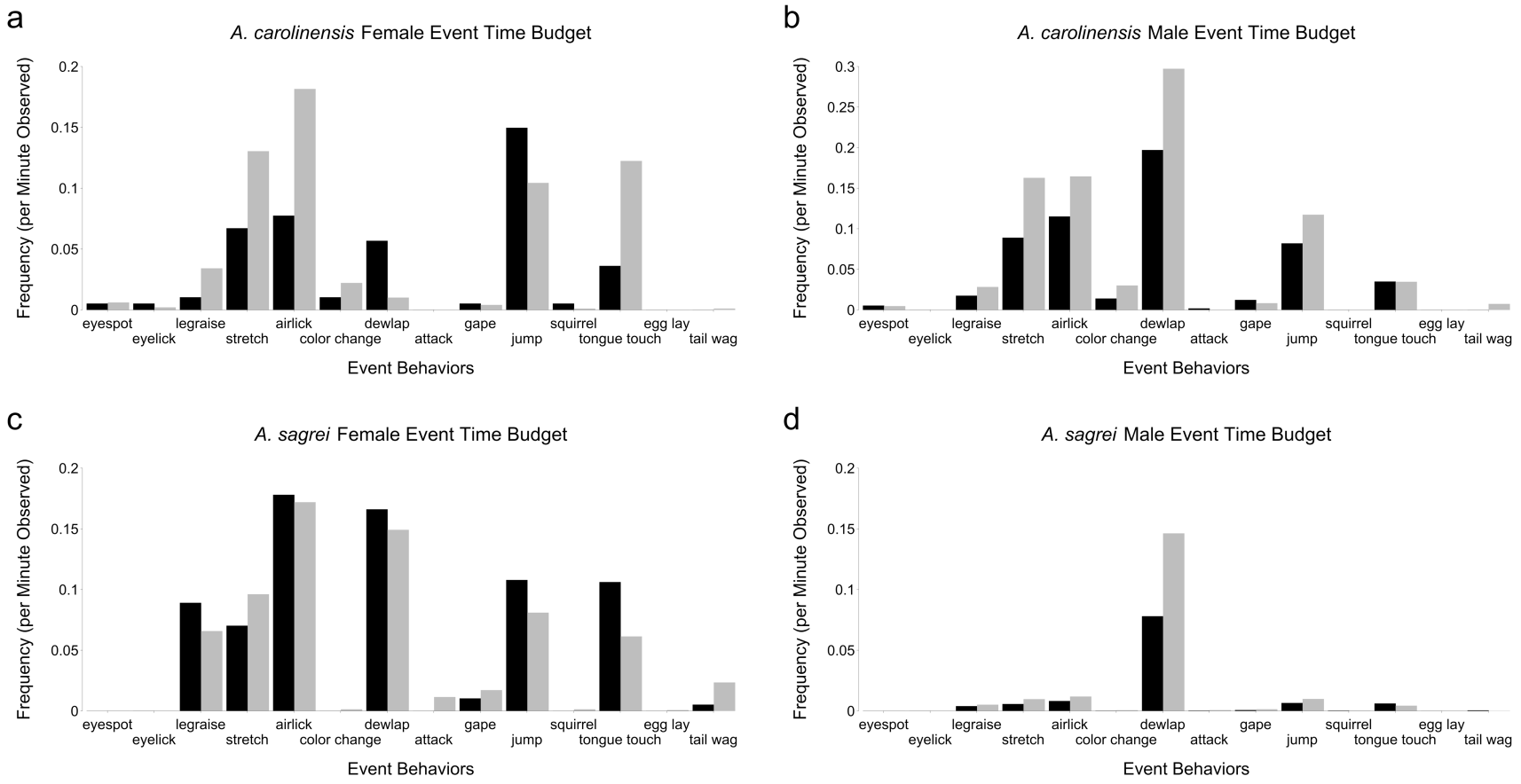

Figure A3. Time budgets including only event behaviors for male and female *A. carolinensis* and *A. sagrei*. The black bars represent the proportion of time engaged in a behavior in the presence of the competitor and the gray bars represent the proportion of time in the absence of the competitor.

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